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Biodiversity, mountains and climate change

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Abstract

BIODIVERSITY, MOUNTAINS AND CLIMATE CHANGE.— This paper discusses the issue of the origin and maintenance of biodiversity on tropical mountains, with emphasis on the Neotropics, and concludes that present-day biodiversity patterns of highland biotas cannot be understood without the combined action of Neogene tectonics and Pleistocene climatic changes.

Key words: climatic changes; diversification; Neogene; Neotropics; orogeny; Pleistocene; speciation.

Resumen

BIODIVERSIDAD, MONTAÑAS Y CAMBIO CLIMÁTICO.— En este artículo se discute el origen y mantenimiento de la biodiversidad en las montañas tropicales, con énfasis en el Neotrópico, y se concluye que los patrones de biodiversidad de las biotas de gran altura no pueden ser explicados sin la acción combinada de la tectónica neógena y los cambios climáticos del Pleistoceno.

Palabras clave: cambios climáticos; diversificación; especiación; Neógeno; Neotrópico; orogénesis; Pleistoceno

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The evolutionary origin of current earth's biodiversity patterns has been a long-standing and controversial topic since the times of Darwin. Emphasis has been placed on the generation and maintenance of the latitudinal biodiversity gradients, with emphasis in the origin of the comparatively high tropical diversity, which has been considered the result of either higher speciation rates (the "cradle" hypothesis), lower extinction rates (the "museum" hypothesis), or the combination of both (the 'out of tropics' hypothesis) (Arita & Vásquez-Domínguez, 2008). Generally, the origin of extant tropical biodiversity is linked to past environmental changes promoting speciation, whereas its maintenance is attributed to ecological mechanisms favoring coexistence thus minimizing extinction (Mittelbach *et al.*, 2007). Concerning the environmental drivers favoring diversification, a controversy has been maintained historically between the defenders of climate changes (mainly the Pleistocene glaciations) and the supporters of pre-Pleistocene (Neogene) tectonically-driven paleogeographical reorganizations (mountain building, sea incursions and retreats, connection and disconnection of land masses, etc.), as primary diversification agents (Moritz *et al.*, 2000). The recent spectacular development of DNA molecular phylogenetic techniques allowing estimation of the age of emergence of extant species has reactivated

the controversy by providing ample support for both Neogene and Pleistocene hypotheses but recent meta-analyses developed on the Neotropics suggest that, rather than conflicting, these hypotheses can be complementary (Rull, 2008; Turchetto-Zollet *et al.*, 2013).

This commentary combines the results and observations of recent literature to show that both tectonics and climate change are needed to explain present-day biodiversity patterns. These works discuss the origin of biological diversity in mountain environments, which support particularly diverse and unique biomes worldwide, especially in tropical latitudes, and may also affect the biodiversity of adjacent lowlands. Emphasis is placed on the Neotropics (Fig. 1).

In a recent paper, Hoorn *et al.* (2013) highlight the role of mountain building in the generation of biodiversity. According to these authors, orogeny may have had direct (waxing and waning of migration barriers and pathways) and indirect (changing drainage patterns, appearance of new high-mountain climates) effects on biotic diversification. Emphasis is placed on the tropical Andes and the potential influence of these mountains on the biodiversity of the adjacent Amazon Basin. Hoorn *et al.* (2013) conclude that "… geological processes related to mountain building have decisively affected biodiversity patterns", which is in line with a former review concluding that current Amazonian biodiversity is deeply rooted in pre-Pleistocene paleogeographic events, notably the Andean uplift that occurred in the Miocene (Hoorn *et al.*, 2010). The same authors dismiss the role of Pleistocene climate changes on Neotropical diversification by claiming that "the Quaternary was a time of distribution shifts, but can no longer be considered a time of diversification in Amazonia", rather, "the Quaternary should possibly be considered as a period of net loss of biodiversity" (Wesselingh *et al.*, 2010).

Another view considers both tectonic reorganizations and climate change as influential drivers in biodiversity generation. Climatic change has generally been considered one of the more powerful evolutionary engines over the entire geological time scale (Erwin, 2009). The combination of changing geographical/topographical patterns and climatic variability at different time scales would have magnified diversification opportunities by creating a complex time-space framework to which Pleistocene glacial cycles may have made a significant contribution (Rull, 2011). This view is based on a previous meta-analysis at the Neotropical level showing that approximately half of the species studied emerged during the Pleistocene and that the other half was of pre-Pleistocene origin (Rull, 2008).

Neotropical mountains may be an excellent laboratory in which to test hypotheses concerning biodiversity generation in relation to paleogeographic reorganization and climate change. In the past, the tropics were generally considered fairly stable regions with respect to climate, even during the Pleistocene. However, it is now known that glacial-interglacial cycles have significantly affected tropical areas and their biotas, especially in mountainous areas. In the Neotropical Andes (Fig. 1), for example, glacial temperature decreases have been estimated to be on the order of 8°C with respect to the present, leading to a downward biotic displacement of up to 1500 m compared to today (Van der Hammen & Cleef, 1986). As a consequence, highland biotas would have experienced successive connections (glacials) and disconnections (interglacials) leading to gene flow and allopatric speciation, respectively, which may have contributed to the shaping of present-day biodiversity patterns (Simpson, 1971).

Until recently, this evolutionary hypothesis was tested against present-day biogeographical patterns, which were suggestive but unable to provide direct and conclusive evidence. However, recently developed DNA phylogenetic tools, especially the possibility of estimating the age of divergence of extant species and relating this age to known paleoenvironmental shifts, has provided more compelling support. For example, a recent study using dated DNA molecular phylogenetics on several extant genera of vascular plants demonstrates that the tropical Andean Highlands (AH) have been an exceptionally active diversification scenario since this mountain range attained its present elevation (Pliocene) and that this diversification has been possible because of Pleistocene climatic fluctuations (Madriñán *et al.*, 2013). Indeed, more than 80 percent of the speciation events (144 out of 177) observed in the AH occurred during the Pleistocene. The average of the estimated speciation rates is 1.36 speciation events per million years.

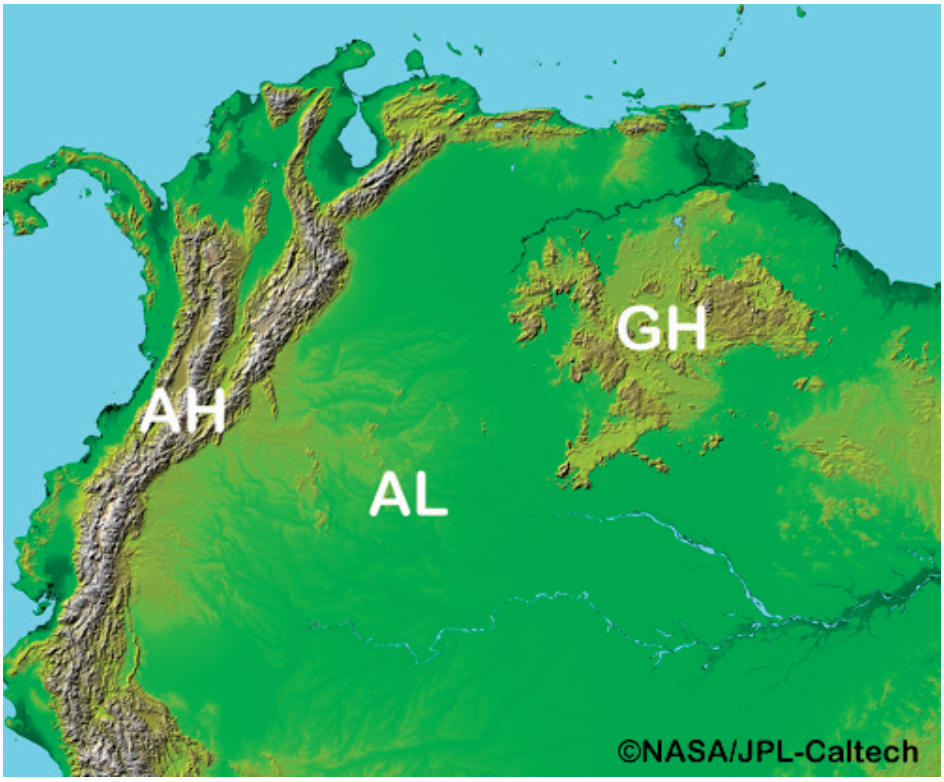

Figure 1. Radar image of northern South America showing the main topographic features discussed in the text. AH: Andean highlands; AL: Amazon Lowlands; GH: Guayana Highlands.

In agreement with Simpson's (1971) hypothesis, it has been suggested that Pleistocene glacial cycles resulted in vertical biotic migrations leading to recurrent contractions (interglacials) and expansions (glacials) of species' ranges, thus favoring allopatric speciation and hybridization, respectively. According to Madriñán *et al.* (2013), the intense Pleistocene speciation recorded at the AH may be indicative of the inability of the involved species to adapt to changing climatic conditions, a hypothesis that should be seriously considered in the face of future climate change.

Other similar cases exist, as for example the DNA phylogeographic study of Hughes & Eastwood (2006), which documents the explosive Pleistocene diversification leading to the emergence of the > 80 extant Andean species of the genus *Lupinus* L. In this case, the speciation rates ranged from 1.93 to 3.72 speciation events per million years. Other studies report equally rapid Pleistocene speciation among other plant genera from the AH, as for example *Aragoa* Kunth, *Calceolaria* L., *Draba* L., *Espeletia* Mutis ex Bonpl. or *Puya* Molina, among others (Vargas & Madriñán, 2012; Nürk *et al.*, 2013). Concerning causes, three main factors have been identified in these studies that could have contributed to the exceptionally high speciation rates: (1) topographic isolation of highland habitats fostering island-like diversification, (2) habitat heterogeneity along steep gradients promoting special adaptations to changing substrates and micro-environmental conditions, and (3) recurrent altitudinal shifts driven by glacial-interglacial cycles leading to range expansions and contractions (i.e. the Simpson hypothesis). Points 1 and 2 are intrinsic to mountain building, whereas point 3, as a global phenomenon, is independent of orogeny. The more reasonable explanation for Pleistocene diversification bursts such as those described above is the interplay of the three mechanisms invoked, as we have empirical evidence for all of them. With the available evidence, there is no reason to dismiss any of these mechanisms or to believe that any of them has been more important than the others, in relation to Pleistocene speciation (Rull, 2011). Concerning extinction, it has been documented that Pleistocene climatic changes have not

contributed to plant elimination, as only a single global extinction and very few of continental extent have been documented for the entire Pleistocene (Willis & Bhagwat, 2009). In the Andes, no any Pleistocene extinction event of plant species has been documented to date. Therefore, as diversification is the balance between speciation and extinction, Pleistocene topographic and climatic changes should be considered net drivers of diversification.

The same diversification model had been proposed earlier for the Guyana Highlands (GH), which are separated from the Andes by the Amazon lowlands (Rull, 2005) (Fig. 1). Unfortunately, the difficulty of obtaining fieldwork permits to develop genetic studies in these mountains has thus far prevented testing of this proposal (Rull & Vegas-Vilarrúbia, 2008). This is especially worrisome if we realize that *ca.* 80 percent of the vascular flora in this biogeographic region, including nearly 400 endemic species, is threatened with extinction by habitat loss in the face of expected climate change by the end of this century (Nogué *et al.*, 2009). Biotic interchange between the Andes and the GH via the Amazon lowlands has also been documented and attributed to the Plio-Pleistocene cooling that initiated the Pleistocene glacial cycles (Noonan & Gaucher, 2005). As a result, climate change may also be viewed as an influential driver for the biotic enrichment of the lowlands, which provides a mechanism for the idea of mountains as "species pumps" (Rull, 2005: Hoorn *et al.*, 2013). Mountains can also act as population-splitting agents and reproductive barriers among lowland plants, thus fostering additional speciation, as would be the case of *Mauritia* L. f. (Rull, 1998). Therefore, mountains would be important for increasing not only the local highland biodiversity but also biodiversity, in general, across the Neotropics.

Patterns and processes similar to those observed in the tropical Andes have been documented in the Mediterranean region, the California Floristic Province and the Hawaiian archipelago (Madriñán *et al.*, 2013), suggesting that the influence of changing climates on mountain diversification may be a global phenomenon. Hoorn *et al.* (2013) argue that "… if there were no mountains in the first place, there would be no alpine species". This statement seems true, but in light of the studies mentioned above, it could be added that topographical changes alone are not enough, and without Plio-Pleistocene climatic changes, the current biodiversity patterns of alpine species would be remarkably lower. Paraphrasing Hutchinson (1965), mountain building modifies the "ecological theater" while climate change is a dynamic element necessary to guide the "evolutionary play". Both are necessary to explain the origin and maintenance of extant biodiversity.

Generally, mountains provide an excellent example of how topographic heterogeneity and climatic change coupled over time may be powerful diversification agents. The present-day biodiversity patterns of the worldwide highland biotas cannot be understood without the synergistic action of tectonic and climatic drivers, especially during the Plio-Pleistocene. Surprisingly, such view is rarely addressed by ecologists working on mountain biodiversity and its potential causes. These researchers are largely focused on present-day elevational gradients and other spatial variables but they usually ignore the potential consequences of time-dependent ecological and evolutionary drivers such as climate changes (e.g. Graham *et al.*, 2014).

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